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Physiological Adjustments to Arid and Mesic Environments in Larks (*Alaudidae*)

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ABSTRACT

Because deserts are characterized by low food availability, high ambient temperature extremes, and absence of drinking water, one might expect that birds that live in these conditions exhibit a lower basal metabolic rate (BMR), reduced total evaporative water loss (TEWL), and greater ability to cope with high air temperatures than their mesic counterparts. To minimize confounding effects of phylogeny, we compared the physiological performance of four species of larks at ambient temperatures (T_a's) ranging from 0° to 50°C: hoopoe larks (*Alaemon alaudipes*) and Dunn's larks (*Eremalauda dunni*) live in hot and dry deserts, whereas skylarks (*Alauda arvensis*) and woodlarks (*Lullula arborea*) occur in temperate mesic areas. Mass-adjusted BMR and TEWL were indistinguishable between hoopoe lark and Dunn's lark and between skylark and woodlark. When grouping the data of the two desert larks in one set and the data of the two mesic larks in another, desert larks are shown to have 43% lower BMR levels and 27% lower TEWL values than the mesic species. Their body temperatures (T_b's) were 1.1°C lower, and the minimal dry heat transfer coefficients (h) were 26% below values for the mesic larks. When T_a exceeded T_b, the h of hoopoe larks and Dunn's larks was high and indistinguishable from h at 40°C, in contrast to the prediction that h should be decreased to minimize heat gain through conductance, convection, or radiation from the environment when T_a exceeds T_b.

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Introduction

Animals that live in deserts might be expected to possess behavioral and physiological adaptations that would enable them to cope with high ambient temperatures (T_a's), low food resources, and lack of drinking water, the main characteristics of these environments (Bartholomew and Cade 1963; Dawson and Schmidt-Nielsen 1964; Williams and Tieleman 2001). Unlike small mammals that are generally nocturnal and as a result do not experience the temperature extremes of the desert environment, desert birds are exposed to T_a's that are among the highest on earth. Shade T_a can exceed 50°C in some deserts, and anecdotal evidence suggests that extreme heat can be a major source of mortality in some bird populations (Serventy 1971). Avian physiological mechanisms that favor survival during extended periods of high T_a's are poorly understood. Exposure to high T_a not only requires heat-tolerance mechanisms but also puts an additional strain on a water and energy balance that already may be compromised by the scarcity of drinking water and food.

Early investigators hypothesized that low primary productivity, high T_a, and absence of drinking water in deserts would select for low levels of basal metabolic rate (BMR) and total evaporative water loss (TEWL) in desert birds but found no general support for this idea (Bartholomew and Cade 1963; Bartholomew 1964; Dawson and Schmidt-Nielsen 1964; Serventy 1971; Dawson 1984). Subsequent studies reported levels of BMR and TEWL below allometric predictions, but because these investigations were often based on a single species, conclusions were tentative (Dawson and Bennett 1973; Weathers 1979; Arad and Marder 1982; Withers and Williams 1990). Across-species comparisons between desert and nondesert species support the hypothesis that arid-zone birds have on average a lower BMR (Tieleman and Williams 2000) and a lower TEWL (Williams 1996).

Broad-scale interspecific comparisons of BMR and TEWL have the inherent interpretational problem that species differ not only in habitat but also in phylogenetic background, diet, and behavior. In addition, knowledge of minimum levels of metabolism and TEWL provides limited understanding of the physiological responses to varying environmental circumstances, including T_a. Restricting comparative analyses to a small group of closely related species occuring in different environments provides the opportunity for a more detailed examination of physiological adjustment while potentially limi-

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ting complications due to markedly different evolutionary history or current dissimilar lifestyles.

At high T_a's, birds increase TEWL to keep their body temperature (T_b) below lethal limits (Calder and King 1974), even when water is in short supply. To minimize evaporative water loss at high T_a's, birds can reduce heat production from metabolism. Another strategy entails minimizing dry heat gain from the environment, quantified by the equation heat gain $= h(T_b - T_a)$, where $T_b - T_a$ is the gradient between the bird's T_b and the environment and h is the dry heat transfer coefficient (Dawson and Schmidt-Nielsen 1966; Hinds and Calder 1973; Weathers and Caccamise 1975; Tieleman and Williams 1999). Influenced by feather insulation, skin vasodilation, surface to volume ratios, and subcutaneous fat reserves, h is a complex variable that combines heat transfer coefficients for conduction, convection, and radiation (Calder and King 1974). The optimal response of h to T_a presumably includes adjustments to minimal levels below the thermoneutral zone, an increase to maximum values when T_a approaches T_b, and a decrease to minimal values again when T_a exceeds T_b (Dawson and Schmidt-Nielsen 1966; Hinds and Calder 1973; Tieleman and Williams 1999).

We hypothesized that increasing aridity selects for gradually decreasing levels of BMR and TEWL in birds and for improved physiological performance under exposure to extreme heat. To test these ideas, we studied the temperature regulation of four closely related birds: Dunn's larks and hoopoe larks from the hyperarid and arid deserts in Arabia and northern Africa and skylarks and woodlarks that live in the mesic temperate zones of Europe and Asia. We determined metabolism, TEWL, dry heat transfer coefficient, and body temperature at T_a's ranging from 0° to 40°C in the mesic birds and from 0° to 50°C in the arid-zone species. We predicted that the desert species would display reduced levels of BMR and TEWL compared with the mesic larks and were capable of controlling their T_b when exposed to high temperatures by a reduced dry heat uptake and/or a rapidly elevated evaporative heat loss when T_a exceeded T_b.

Material and Methods

We mist-netted hoopoe larks (*Alaemon alaudipes*, mass 37.7 ± 2.72 g, $n = 7$) and Dunn's larks (*Eremalauda dunni*, 20.6 ± 1.60 g, $n = 16$) in Mahazat as-Sayd, a reserve in the Arabian Desert (N 22°15′, E 41°50′), and housed them in outdoor aviaries at the National Wildlife Research Center (NWRC), near Taif, Saudi Arabia. Average yearly rainfall in Mahazat equals 90 mm, and the maximum T_a in July averages 40.2°C with some daily maxima reaching 50°C (NWRC, unpublished data). In the Netherlands, we caught skylarks (*Alauda arvensis*, 31.7 ± 2.85 g, $n = 15$) and woodlarks (*Lullula arborea*, 25.5 ± 1.03 g, $n = 14$) in the province of Drenthe (N 52°52′, E 06°20′) and kept them in outdoor aviaries at the Zoological Laboratory of the University of Groningen. In our study area in the Netherlands, rainfall averages 750 mm yr^{-1}, and mean maximum T_a in July is 21.7°C (Koninklijk Nederlands Meteorologisch Instituut). We measured metabolism and TEWL of all birds after they had been in captivity for 3–6 wk during June, July, or August of 1998–2001. Larks in Arabia were fed ad lib. with mealworms, crickets, cockroaches, and seeds, whereas larks in the Netherlands had access to ad lib. water and food similar to that available for the Arabian birds, with the addition of chopped raw heart.

To measure the phylogenetic relatedness between hoopoe lark, Dunn's lark, skylark, and woodlark, we determined nucleotide sequences of the cytochrome *b* and the 16S rRNA genes of the mitochondrial DNA. Skylarks and woodlarks showed a sequence divergence of 5.0%, Dunn's larks were related to the skylark/woodlark group by a 5.6% divergence, and hoopoe larks were basal in this phylogeny with a 8.9% divergence from the clade that contains the previous three species (B. I. Tieleman, J. B. Williams, and P. Bloomer, unpublished data).

We measured rates of oxygen consumption ($\dot{V}O_2$'s) and TEWL for postabsorptive birds during their nocturnal phase by standard flow-through respirometry and hygrometry methods (Gessaman 1987). Birds in Saudi Arabia were placed in water-jacketed steel metabolic chambers (24 × 20 × 28 cm) that had an air-tight Plexiglas lid. During measurements, T_a in the chamber was controlled by a Neslab circulating water bath (RTE-140) to within 0.2°C. Larks in the Netherlands were placed in steel metabolic chambers of identical dimensions where T_a was controlled by a Heraeus Vötsch environmental chamber. Birds were placed on a wire-mesh platform over a layer of mineral oil that trapped feces in order to exclude it as a source of water in the measurements. In Saudi Arabia, we used a positive pressure system for the hoopoe lark measurements and a negative pressure system for the Dunn's lark measurements, and in the Netherlands, we used a negative pressure system for skylark and woodlark. In the positive pressure system, air coursed through columns of drierite, soda lime, and drierite to remove water and CO_2 from the air stream, through a previously calibrated (Levy 1964) Brooks mass flow controller (model 5850E) set between 500 and 1,700 mL min^{-1} (STP), depending on species, and T_a, then through the chamber. Exiting air passed through a General Eastern dewpoint hygrometer (M4-DP). A subsample was then routed through silica gel, ascarite, and silica gel before being passed into an Applied Electrochemistry oxygen analyzer (S3A-II) that determined the fractional concentration of oxygen in dry, CO_2-free outlet air. Our negative pressure system consisted of air coursing through Drierite, soda lime, and Drierite, the chamber, the dewpoint hygrometer, and again through Drierite, soda lime, and Drierite, before passing through the mass flow controller, a diaphragm pump, and into an overflow from which the O_2-analyzer sampled air (Applied Electrochemistry S3A-II in Saudi Arabia; Servomex Xentra 4100 in the Netherlands). After a 2–3-h equil-

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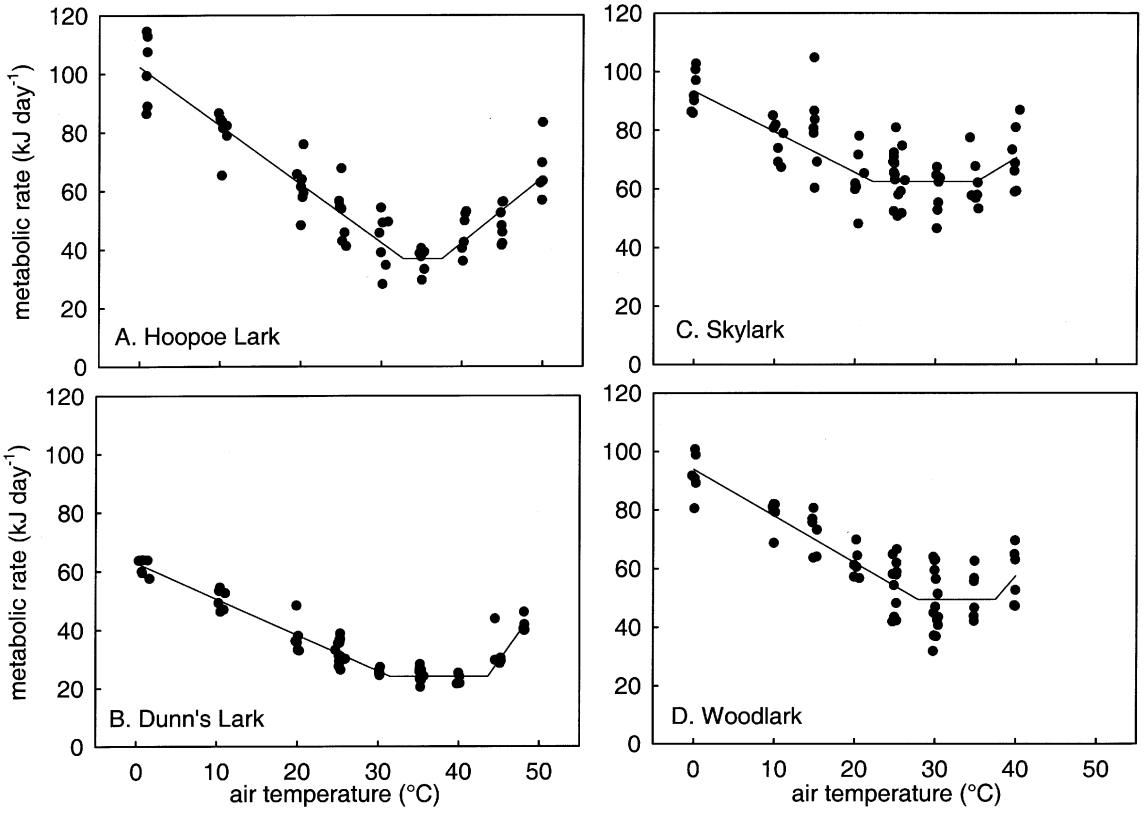

Figure 1. Metabolic rate as a function of air temperature in hoopoe lark (*A*), Dunn's lark (*B*), skylark (*C*), and woodlark (*D*)

ibration period, we recorded the oxygen concentration and dewpoint of inlet and outlet air, the temperature of the dewpoint hygrometer, and T_a in the chamber, using a Campbell Scientific data logger, model 21X or CR23X. Outlet air had a relative humidity that was always below 25% (Lasiewski et al. 1966) and an oxygen concentration between 20.55% and 20.85%. Oxygen consumption was calculated with equation (2) of Hill (1972) for the positive pressure system and with equation (4a) of Withers (1977) for the negative pressure system. We used 20.08 J mL^{-1} O_2 to convert oxygen consumption to heat production (Schmidt-Nielsen 1997). When, during the third hour of measurements, the traces for oxygen consumption and dewpoint were stable for at least 10 min, we noted these times and used these data for calculations. For measurements of hoopoe larks at 50°C and of Dunn's larks at 48°C, we equilibrated birds for 2 h at 40°C before increasing the T_a to 50°C or 48°C, respectively, and took our measurement after a 45-min period of exposure to these high T_a's. We did not measure skylarks and woodlarks at T_a's exceeding 40°C because, judging from the heavy panting, birds were visibly heat-stressed at 40°C, and we did not want to risk mortality.

Evaporative water loss was calculated using the equation TEWL (g d^{-1}) = $[(V_e\rho_{out} - V_i\rho_{in})] \times 1.44 \times 10^{-3}$, where ρ_{in} and ρ_{out} are the absolute humidities (g H_2O m^{-3}) of inlet and outlet air, V_i is the flow rate (mL min^{-1}) of air entering the chamber, and V_e is the flow rate of exiting air. Absolute humidity (STP) was determined with the equation ρ (g m^{-3}) = $[216.7e_s/(T_{dp} + 273.15)] \times [P_0(T_{dp} + 273.15)] / [P_a (T_0 + 273.15)]$, where e_s is the saturation vapor pressure (mbar) at a given dewpoint, T_{dp} is the temperature (°C) of the air in the dewpoint hygrometer, P_0 is standard pressure (1,013 mbar), P_a is barometric pressure (mbar), and T_0 is standard temperature (0°C). We calculated V_e and V_i following Williams and Tieleman (2000) for the positive pressure system. For the negative pressure system, we calculated $V_i = V_{\text{flow controller}} + \dot{V}O_2$, and $V_e = V_{\text{flow controller}} + 0.71(\dot{V}O_2) + \dot{V}H_2O$. In this equation, $V_{\text{flow controller}}$ (mL min^{-1}), the flow rate through the mass flow controller, and oxygen consumption ($\dot{V}O_2$; mL min^{-1}) are known, R.Q is assumed to equal 0.71 (King and Farner 1961), and $\dot{V}H_2O$ is calculated as $\dot{V}H_2O = \rho(V_{\text{flow controller}} + \dot{V}CO_2)/(1 - \rho)$. The latter equation is derived from the absolute humidity $\rho = \dot{V}H_2O/(V_{\text{flow controller}} + \dot{V}CO_2 + \dot{V}H_2O)$, the fraction of water in air flowing through the dewpoint hygrometer.

After completing the metabolism measurements, we immediately measured the T_b of birds with an Omega thermometer and a 36-gauge copper-constantan thermocouple. Because

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Table 1: Metabolic rate as a function of T_a for hoopoe lark, Dunn's lark, skylark, and woodlark

Species	a (SE)	b	n	r^2	P	T_{lc}	T_{uc}	BMR (kJ d^{-1} [SD])
Hoopoe lark:								
$<T_{lc}$	−2.00 (.15)	102.21	34	.85	<.001	32.7	37.5	36.87 (3.97)
$>T_{uc}$	2.22 (.51)	−46.41	18	.54	.001			
Dunn's lark:								
$<T_{lc}$	−1.23 (.06)	62.78	40	.92	<.001	31.5	43.6	24.01 (1.87)
$>T_{uc}$	3.89 (.43)	−145.48	10	.91	<.001			
Skylark:								
$<T_{lc}$	−1.39 (.21)	93.34	27	.64	<.001	22.2	35.1	62.41 (8.43)
$>T_{uc}$	1.66 (1.02)	4.11	14	.18	.13			
Woodlark:								
$<T_{lc}$	−1.61 (.14)	93.81	37	.80	<.001	27.6	35–40	49.39 (9.96)

Note. The equations are in the form of metabolic rate (kJ d^{-1}) = $a \times T_a + b$. Average basal metabolic rates (BMR ± SD) are based on the following numbers of observations (n; N is the number of individuals): hoopoe lark $n = 7$, $N = 7$; Dunn's lark $n = 22$, $N = 16$; skylark $n = 29$, $N = 14$; woodlark $n = 20$, $N = 14$. T_k is the lower critical temperature and T_{uc} is the upper critical temperature of the thermoneutral zone.

we did not have continuous recordings of T_b, we calculated the dry heat transfer coefficient h as $h = (M - E)/(T_b - T_a)$, and we assumed that the change in T_b during our measurements (dT_b/dt) was 0 (Tieleman and Williams 1999). In this equation, M equals metabolic heat production and E is evaporative heat loss. At $T_a = T_b$, we calculated h with l'Hôpital's rule (Tieleman and Williams 1999).

ANOVA and post hoc tests were carried out using GLM procedures in SPSS 10.0. Averages are reported ± 1 SEM, unless noted otherwise. Experiments were performed under license of the University of Groningen (DEC 2425).

Results

For all species of larks, metabolic rate as a function of T_a had the general shape of the Scholander model, with increased levels of metabolism below and above a distinct thermoneutral zone, where levels of metabolism were lower in the two desert species than in the two mesic birds (Fig. 1; Table 1). The lower and upper critical T_a's of the two mesic larks were lower than those of the two desert species (Table 1). We used ANOVA with body mass as covariate and species as fixed factor to compare BMR among the four species, and we found no significant effect of the interaction between body mass and species ($F_{3,70} = 0.75$, $P = 0.52$) but a significant effect of species on BMR ($F_{3,51} = 51.42$, $P < 0.001$). To test for differences in mass-adjusted rates of BMR, we divided BMR by mass$^{0.940}$, where 0.940 is the exponent of an allometric equation of 14 species of larks (B. I. Tieleman and J. B. Williams, unpublished manuscript). Mass-adjusted rates of basal metabolism (n as in Table 1) were indistinguishable between hoopoe lark (1.21 ± 0.14 kJ d^{-1} $g^{-0.940}$) and Dunn's lark (1.41 ± 0.08 kJ d^{-1} $g^{-0.940}$, Tukey test $P = 0.64$) and between woodlark (2.35 ± 0.08 kJ d^{-1} $g^{-0.940}$) and skylark (2.43 ± 0.07 kJ d^{-1} $g^{-0.940}$, Tukey test $P = 0.91$) but differed in comparisons of the other species pairs (Tukey test $P < 0.001$). We concluded that BMR of the arid-zone larks was 43% lower than that of the mesic species.

All larks maintained relatively constant minimum levels of TEWL at low T_a's and rapidly increased TEWL at higher T_a's (Fig. 2).When we compared TEWL at 25°C using ANCOVA with body mass as covariate and species as fixed factor, we found that the interaction term was not significant ($F_{3,44} = 2.13$, $P = 0.11$) but that species had a significant effect in the model ($F_{3,47} = 7.88$, $P < 0.0001$). We calculated mass-adjusted TEWL by dividing TEWL by mass$^{0.883}$, where 0.883 is the exponent of an equation relating TEWL to body mass of 14 species of larks (B. I. Tieleman and J. B. Williams, unpublished manuscript), and performed a post hoc test to determine differences between species. Mass-adjusted TEWL was significantly different between hoopoe larks (0.104 ± 0.0096 g d^{-1} $g^{-0.883}$, $n = 7$) and skylarks (0.166 ± 0.011 g d^{-1} $g^{-0.883}$, $n = 15$, Tukey test $P = 0.007$) and between Dunn's larks (0.119 ± 0.010 g d^{-1} $g^{-0.883}$, $n = 16$) and skylarks (Tukey test $P = 0.010$) but were indistinguishable in the remaining pairwise comparisons (Tukey test $P > 0.23$). Mass-adjusted TEWL of woodlarks (0.138 ± 0.010 g d^{-1} $g^{-0.883}$, $n = 14$) was intermediate between skylarks on the one hand and hoopoe larks and Dunn's larks on the other. Combining mass-adjusted TEWL for the two arid birds and for the two mesic larks, the two arid-zone larks had a mass-adjusted TEWL at 25°C that was on average 27% lower than that of the two mesic species. We performed a similar analysis for TEWL at 40°C and found no significant interaction between body mass and species ($F_{3,17} = 0.46$, $P = 0.72$) but a significant effect of species ($F_{3,20} = 17.42$, $P < 0.0001$). Post hoc analysis of mass-adjusted TEWL showed no significant difference between hoopoe lark and Dunn's lark (Tukey test $P = 0.15$) or between skylark and woodlark (Tukey test $P = 0.84$) but significant differences be-

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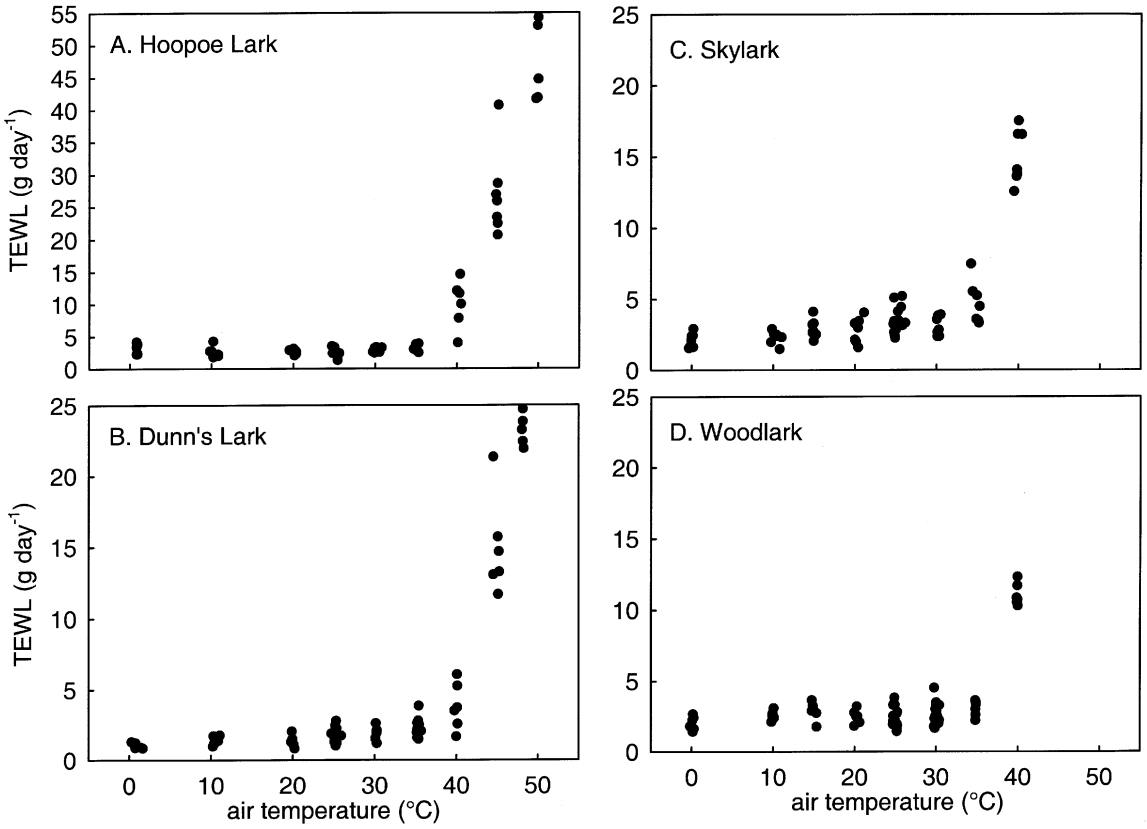

Figure 2. TEWL as a function of air temperature in hoopoe lark (*A*), Dunn's lark (*B*), skylark (*C*), and woodlark (*D*)

tween all pairs of arid and mesic species (Tukey test $P < 0.005$). With rising T_a, the two mesic larks, skylark and woodlark, started increasing their TEWL at lower T_a than the two species from the desert. Using TEWL at 25°C as baseline, we found that skylark and woodlark augment TEWL at 40°C by factors of 4.3 and 4.6, respectively, whereas hoopoe lark and Dunn's lark increase TEWL by 3.9 and 2.2, respectively.

In all four species of larks, T_b was fairly constant at T_a's up to 35°C but increased at higher T_a's (Fig. 3). We tested if T_b at T_a's up to 35°C varied between species using ANOVA with species and T_a as fixed factors. The interaction between T_a and species and T_a had no significant effects on T_b, but T_b differed significantly between species (interaction $F_{15,158} = 1.00$, $P = 0.46$; T_a $F_{6,173} = 1.23$, $P = 0.29$; species $F_{3,173} = 19.10$, $P < 0.001$). Post hoc contrast analysis of the type "repeated" showed no significant difference between hoopoe and Dunn's larks (contrast 0.17 ± 0.20, $P = 0.40$) or between skylarks and woodlarks (contrast 0.06 ± 0.21, $P = 0.76$). Comparing the two arid species with the two mesic larks revealed a T_b that was on average 1.1°C higher in the latter group ($F_{1,175} = 56.87$, $P < 0.001$). At $T_a = 40$°C, T_b's of the different species were indistinguishable ($F_{3,21} = 2.41$, $P = 0.10$).

The heat transfer coefficients of hoopoe lark, Dunn's lark, skylark, and woodlark were minimal and constant at low T_a's and increased rapidly with increasing T_a in the thermoneutral zone up to 40°C (Fig. 4). To test if h differed between species and between the T_a's, we performed an ANCOVA with mass as covariate and species and T_a as fixed factors. We included T_a's of 20°C when h was minimal for all species and T_a's of 40°C when h was maximal at the highest T_a with data for all species. After removing the insignificant interactions between the fixed factors and the covariate from the model, we found a significant interaction between species and T_a and significant effects of species and T_a but no significant effect of mass on h (interaction $F_{3,41} = 3.93$, $P = 0.015$, species $F_{3,41} = 6.04$, $P = 0.002$, T_a $F_{1,41} = 86.62$, $P < 0.0001$, mass $F_{1,41} = 0.45$, $P = 0.51$). To investigate in more detail differences in minimal h between species, we performed an ANCOVA for h at 20°C and found that the interaction between mass and species was not significant but that species and mass had significant effects on h (interaction $F_{3,18} = 0.24$, $P = 0.87$; species $F_{3,21} = 8.75$, $P = 0.001$; mass $F_{1,21} = 6.45$, $P = 0.019$). To test which species differed from each other, we performed a post hoc contrast analysis that showed no significant difference in h between the

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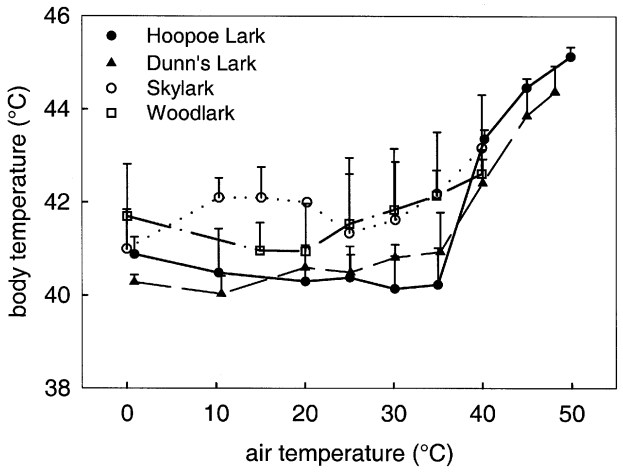

Figure 3. Body temperature (±1 SD) as a function of air temperature in hoopoe lark, Dunn's lark, skylark, and woodlark.

skylark and the woodlark (contrast 0.090 ± 0.35 kJ d^{-1} $°C^{-1}$, $P = 0.80$) or between the hoopoe lark and the Dunn's lark (contrast 0.54 ± 0.68 kJ d^{-1} $°C^{-1}$, $P = 0.44$) but a significant difference between woodlark and hoopoe lark (contrast 1.14 ± 0.52 kJ d^{-1} $°C^{-1}$, $P = 0.042$). When we combined the data for skylark and woodlark, the mesic species, and for hoopoe lark and Dunn's lark, the arid birds, environment had a highly significant effect on minimal h ($F_{1,23} = 26.79$, $P < 0.0001$). For a hypothetical 30-g lark from a mesic environment, minimal h would be 3.07 kJ d^{-1} $°C^{-1}$, whereas for a bird from arid regions, this value would equal 2.26 kJ d^{-1} $°C^{-1}$, 26% lower. Using Meeh's equation to estimate body surface (Walsberg and King 1978), we also calculated surface-specific h for all birds at 20°C. Average surface-specific h was 3.69 ± 0.71 (SD) W m^{-2} $°C^{-1}$ ($n = 7$) for skylarks, 3.59 ± 0.32 (SD) W m^{-2} $°C^{-1}$ ($n = 6$) for woodlarks, 2.79 ± 0.42 (SD) W m^{-2} $°C^{-1}$ ($n = 7$) for hoopoe larks, and 2.53 ± 0.29 (SD) W m^{-2} $°C^{-1}$ ($n = 6$) for Dunn's larks.

We performed an identical series of analyses for h at 40°C. The ANCOVA resulted in a significant effect of species ($F_{3,19} = 4.49$, $P < 0.015$), and the consecutive post hoc test revealed a significant difference between woodlark and hoopoe lark (contrast 4.31 ± 1.95 kJ d^{-1} $°C^{-1}$, $P = 0.040$) but no significant differences between woodlark and skylark (contrast 2.65 ± 2.12 kJ d^{-1} $°C^{-1}$, $P = 0.23$) or between hoopoe lark and Dunn's lark (contrast 2.05 ± 2.32 kJ d^{-1} $°C^{-1}$, $P < 0.39$). Combining data for the two mesic and for the two arid birds, we found a significant effect of environment ($F_{1,21} = 9.07$, $P < 0.007$). A hypothetical 30-g lark from a mesic area would have a h at 40°C of 10.06 kJ d^{-1} $°C^{-1}$, and a lark from arid environments would possess a h 40% lower, 6.05 kJ d^{-1} $°C^{-1}$.

Hoopoe larks and Dunn's larks did not decrease h when T_a exceeded T_b, contra the expectation that birds should decrease the dry heat uptake at these T_a's (Fig. 4*A*, 4*B*). For hoopoe larks, h at 50°C was indistinguishable from h at 40°C (paired $t = 2.16$, df = 4, $P = 0.10$), and for Dunn's larks, h at 48°C was not significantly different from h at 40°C ($t = 1.77$, df = 9, $P = 0.11$).

Discussion

This study of the physiological adjustments of four closely related species of larks, two from hot and dry deserts and two from mesic temperate areas, supports the idea that within the lark family, desert species have reduced levels of BMR and TEWL compared with their mesic counterparts. Categorizing hoopoe larks and Dunn's larks as desert species and woodlarks and skylarks as mesic birds, mass-adjusted BMR of arid-zone larks was 43% lower than that of mesic larks and mass-adjusted TEWL was reduced by 27% in desert species. The magnitude of these differences was larger than the 17% decrease in BMR (Tieleman and Williams 2000) but smaller than the 35% decrease in TEWL (Williams 1996) reported in multispecies comparisons for lark-sized desert birds. When compared with an allometric equation for BMR based on all birds (Tieleman and Williams 2000), hoopoe larks and Dunn's larks exhibited BMR values 3% and 7% below predictions, whereas skylarks and woodlarks surpassed predictions by 83% and 67%. In comparison with predicted values of TEWL from an equation for all birds (Williams 1996), TEWL of hoopoe lark and Dunn's lark were 27% and 28% lower, and values for skylark and woodlark were 11% above and 11% below predictions, respectively.

Although several mechanisms that influence BMR have been identified, an integrative understanding of the wide variation in BMR between species of similar body size remains elusive. Gaps in our knowledge include the genetic basis of BMR (Konarzewski and Diamond 1995) and the extent to which presumably genetically programmed levels of BMR can be adjusted by acclimatization to the environment. Acclimatization to the environment has been reported in studies of seasonal variation in BMR (Kendeigh 1969; Pohl and West 1973; Cooper and Swanson 1994) and in studies that temporarily expose birds to different temperatures (Gelineo 1964; Hudson and Kimzey 1966; Chaffee and Roberts 1971; Williams and Tieleman 2000). In nine studies of temperate-zone birds, BMR increased on average by 32% ± 7.8% when birds were transferred from warm (29°–33°C) to cold environments (0°–15°C) and kept there for 3–4 wk (Gelineo 1964). When hoopoe larks were exposed to 35°C and 15°C for 3 wk, birds from the 35°C group had a 30% lower BMR than birds from the 15°C group, an indication that the difference in BMR between larks from mesic and arid areas may be at least partially attributable to acclimatization (Williams and Tieleman 2000). The extent to which mesic larks are capable of decreasing BMR when exposed to high T_a's remains to be quantified. Important determinants of BMR appear to

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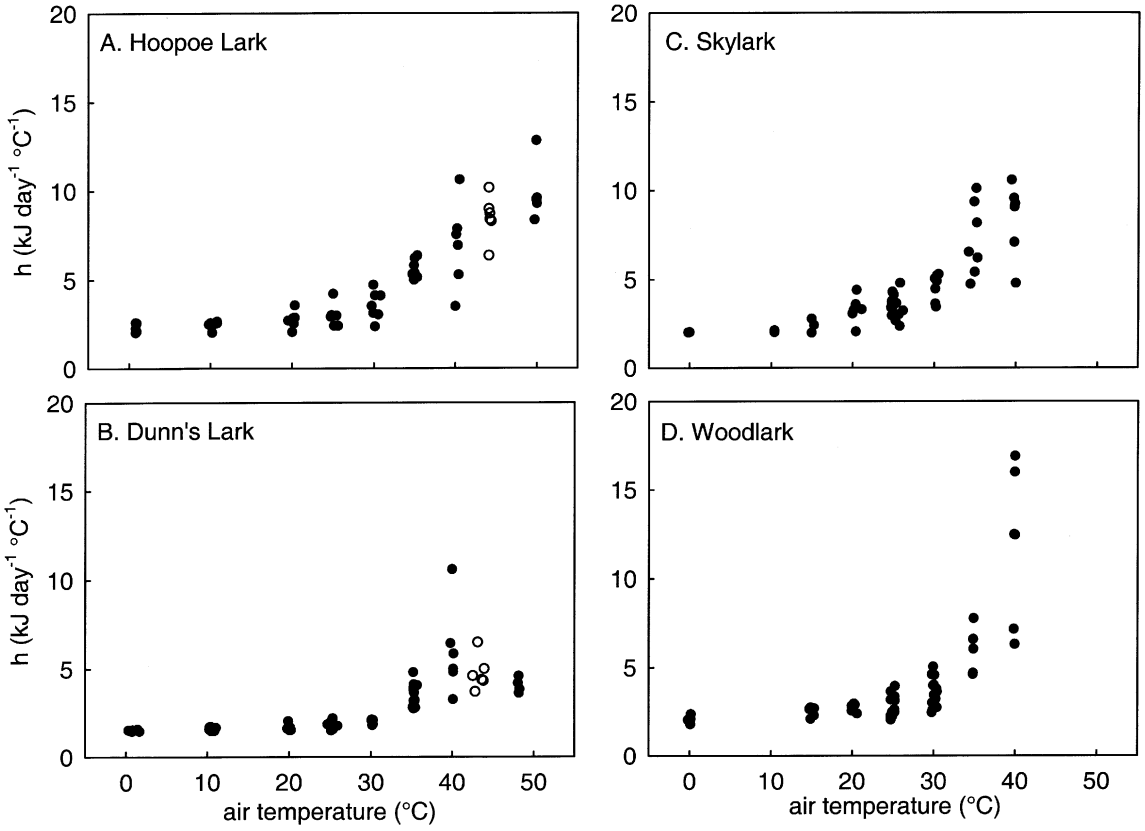

Figure 4. Dry heat transfer coefficient as a function of air temperature in hoopoe lark (*A*), Dunn's lark (*B*), skylark (*C*), and woodlark (*D*). Unfilled circles are calculated using l'Hôpital's rule.

be the size of internal organs, especially the heart, kidney, liver, and intestines (Daan et al. 1990; Chappell et al. 1999; Williams and Tieleman 2000). One may expect that selection pressures for low food requirements, low water loss, and low heat-transfer coefficients in desert birds have led through dynamic optimization to relatively small ratios of BMR and metabolic organ size to body mass.

Mechanisms that determine TEWL have received less attention than those that affect BMR despite the crucial importance of water loss in the maintenance of water balance for terrestrial vertebrates. The adaptive significance of TEWL is likely to be essential especially for survival in the most extreme terrestrial environments, deserts. TEWL is the sum of respiratory and cutaneous water losses, and differences in TEWL between species could be due to variation in respiratory variables and/or skin resistance to water vapor. When hoopoe larks were exposed to 35°C and 15°C for 3 wk, the 35°C group had a TEWL 30% below that of the 15°C group, suggesting a potential role for phenotypic plasticity in explaining differences between desert and nondesert birds (Williams and Tieleman 2000). A property potentially explaining the differences in TEWL between arid and mesic birds and allowing for a flexible response to environment is the composition and structure of the stratum corneum of the skin that may influence cutaneous water loss (Arad et al. 1987; Webster and Bernstein 1987; Menon et al. 1989, 1996; Peltonen et al. 1998).

Reduced BMR and TEWL in the two desert lark species were accompanied by a lower setpoint of T_b at T_a up to 35°C, compared with the larks from mesic areas. At 40°C, T_b's of arid and mesic species were similar. A low T_b might result from a low rate of metabolism, which we found in the hoopoe larks and Dunn's larks, and from a high dry heat loss, not supported by our data, which showed a larger h in the mesic species than in the arid larks. Although a high T_b might be useful for desert animals to facilitate dry heat loss by increasing the temperature difference between animal and environment, there is no evidence that desert birds have higher T_b than nondesert species (Tieleman and Williams 1999). In fact, one could imagine that a low T_b is beneficial because animals have a larger buffer to store heat before reaching lethal temperatures, assuming that the latter are similar in desert and nondesert animals (McNab and Morrison 1963).

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Reciprocal transplantation experiments where animals are exposed to conditions of the other species' environment may give insights into physiological performance that cannot be gained from comparisons of minimal metabolism and TEWL. Exposure to a range of T_a's showed that the two larks from the desert have higher lower and upper critical T_a's than the two mesic species (Table 1). In the field, all four species experience T_a's below or above their thermoneutral zones on a daily basis. The high lower critical T_a will force the desert species to increase metabolism when T_a's are still fairly high, but the low heat transfer coefficient enables them to increase their metabolism by a relatively small amount compared with the mesic birds once they experience T_a's below the thermoneutral zone. At $T_a = 40$°C, the mesic birds markedly increased their TEWL, whereas the desert species maintained TEWL at low levels (Fig. 2). Interindividual variation in h is larger at this T_a (Fig. 4), but on average, h was 40% lower in the desert birds. The resulting low dry heat loss combined with the low evaporative heat loss suggests that desert birds are better able to cope with a T_a of 40°C because they have a lower metabolic heat production than mesic birds and therefore do not need to dissipate as much heat through either evaporation or avenues of dry heat loss.

At $T_a = T_b$, birds can no longer dissipate heat through conductance, convection, or radiation and must rely on evaporative cooling to prevent overheating. Describing the response of h at these high T_a's has been problematic because at $T_a = T_b$, the denominator of h, $T_b - T_a$, and the numerator $M - E$ are zero, and h cannot be calculated directly. However, with the use of l'Hôpital's rule, a differentiation technique, we calculated a polynomial approximation of h (Tieleman and Williams 1999) and found that hoopoe larks and Dunn's larks did not decrease h once T_a reached T_b (*unfilled symbols*, Fig. 4*A*, 4*B*). At higher T_a's, values of h remained high and indistinguishable from those at 40°C. These results do not support the prediction that birds should minimize h when T_a exceeds T_b to minimize heat gain from the environment in order to reduce the costly loss of water for evaporative cooling. These patterns are similar to findings of h at high T_a's for other small birds, like black-rumped waxbill (*Estrilda troglodytes*), black-throated sparrow (*Amphispiza bilineata*), monk parakeet (*Myiopsitta monachus*), and dune lark (*Mirafra erythrocephalus*; Cade et al. 1965; Weathers and Caccamise 1975; Weathers 1981; Tieleman and Williams 1999; Williams 1999).

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